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Studies on the Parasitic Helminths of the North Central States. II. Helminths of Voles (*Microtus* spp.) Preliminary Report

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The helminths of North American mouse-like rodents have received little study. Previous work has been based on low numbers of animals examined, and there has been little reference to the ecology involved. The purpose of this paper is to present data resulting from the examination of over 600 voles, with special reference to host-parasite relationships.

Hall (1916) reviewed the nematodes parasitic in rodents, and previous records of helminths from voles are contained in the papers of Harkema (1936) and Erickson (1938). In addition to these, a number of new species has been described. No effort has been made here to list all helminths previously recorded from voles, and only those of interest in connection with the present work are mentioned.

Rodents of the genus *Microtus* are of much economic importance in connection with agriculture, and for this reason have been given considerable attention. The fluctuations of vole populations have long been observed, and a considerable amount of effort has been spent in attempts to explain their population behavior. The bionomics of voles has been investigated both in North America and in Eurasia. The work of Hamilton (1937, 1941) in the eastern United States has been especially complete, as has that of Elton and his co-workers in Europe. Much work on the ecology of rodents has been done in Russia, some of which has been reviewed by Kalabukhov (1935), and by Elton (1942). Unfortunately, the Russian work has not been generally available.

Voles lend themselves especially well to studies concerned with population fluctuations, since the rise and fall of their numbers seems to occur within a span of three or four years, in contrast to that of certain other species (snowshoe hare, ruffed grouse, and others), which have a cycle of about 10 years.

In spite of their availability in considerable numbers, wide geographical distribution, and interesting population behavior, very little has been done in the way of host-parasite studies with voles. The work of Kirschenblatt (1938), concerning *Microtus socialis satunini* Ogn., *M. socialis schidlovskyi* Arg., and *M. arvalis transcaucasicus* St., as well as other rodents in the

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Transcaucasus region, is of especial interest. We were able to obtain this paper only in late 1947, through the kindness of Dr. Charles Elton, as it does not appear to be available in North America. An effort has been made to include the points in Kirschenblatt's work which are of interest in connection with the present paper. According to Dr. H. A. Baylis (personal communication), voles in the British Isles have not been found parasitized by helminths to a degree adequate to allow a profitable study of this type. Elton and his associates (1931) carried out such a study with the woodmouse, *Apodemus sylvaticus* L., a form in some ways comparable to the North American *Peromyscus*.

METHODS AND SOURCES OF MATERIAL

The procedure for collecting helminths was the same as that used in a previous study (Rausch and Tiner, 1948). After the voles were weighed, the viscera were removed, and each organ was opened separately in a clean dish of water. The contents of each viscus were examined under the low power of the dissecting microscope, after any macroscopic forms present had been removed. It should be noted here that all the animals examined were in a fresh condition; in the opinion of the writers, carcasses preserved in formalin do not give satisfactory results, although the use of preservatives may be necessary under some circumstances. After their isolation, the helminths were fixed in formalin-acetic acid-alcohol solution, and handled in the usual manner.

Voles were ordinarily captured by means of snap mouse traps, set directly in the runways. Baited traps were rarely used.

The collecting was done entirely by the senior author from 1942 to 1945. From 1945 to 1948, assistance was given by the junior author, and by other persons as noted in the acknowledgment. Some of the latter, particularly Messrs. L. H. and C. F. Troesch, have lent their assistance on occasion since the inception of this study. The Wisconsin collecting, in connection with this study, was done by the senior author.

The present study is concerned mainly with a general survey of the helminths parasitic in voles, and with more intensive work carried out locally in two areas.

For the survey work, voles were obtained from wherever possible, and specimens were secured from the states of Ohio, Indiana, Illinois, Michigan, and Wisconsin. The number of animals from Indiana and Illinois, however, was relatively small. A few voles were examined from Manitoba, in addition to those from the North Central States region. While the Manitoba specimens do not come under the scope of this study, helminth records from them are included in order to give all possible information on distribution.

A total of 648 voles has been examined. Of these, 570 were *Microtus p. pennsylvanicus* Ord; 46 were *M. ochrogaster* Wagner; and 32 were *M. pennsylvanicus drummondii* (Audubon and Bachman).

The localities in the North Central States region from which voles have

been obtained are shown in Figure 1, according to county in which they were found. These counties, as numbered on the map, are as follows:

WISCONSIN
1. Vilas
2. Fond du Lac
3. Sheboygan
4. Dodge
5. Dane
6. Waukesha
7. Milwaukee

ILLINOIS
8. Cook
9. Hancock
10. Mason
11. Piatt
12. Champaign
13. Vermilion
14. Saline

INDIANA
15. Tippecanoe

MICHIGAN
16. Cheboygan
17. Ingham
18. Washtenaw

OHIO
19. Preble
20. Franklin
21. Union
22. Marion
23. Morrow
24. Lorain
25. Geauga

Of the two local intensive studies, one was carried out in Ingham County, in southern Michigan (Figure 1, county 17). A fairly uniform field of about 23 acres, adjoining, on the west side, an extensive woodlot, was used.

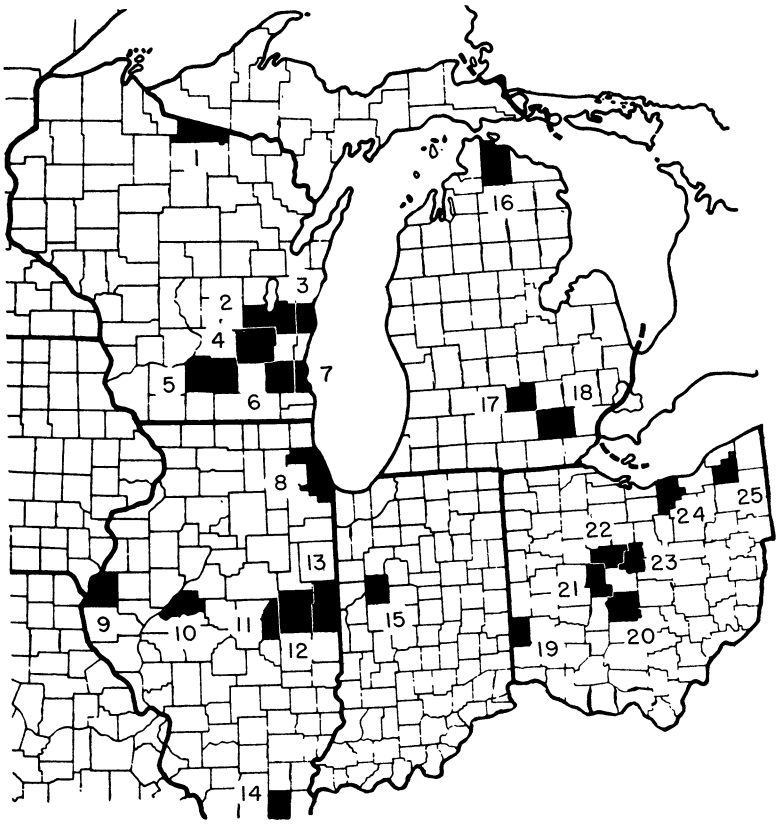

Fig. 1.—Map of the North Central States region, showing counties from which voles were collected.

An open woodlot about 50 yards wide ran across the south side of the field, while the other two sides bordered cultivated fields. The vegetation of the area consisted of blue grass, *Poa* sp., with several species of annuals interspersed. Hawthorne bushes, *Crataegus* sp., were distributed throughout, as were small areas of prickly ash, *Zanthoxylum americanus* L., and *Vibernum* sp. Certain moist areas supported heavy growths of *Carex* sp., which also appeared to be good vole habitat, especially during the winter. As far as could be determined, the vole population was uniform over the area when the study was begun. The field was grazed by cattle during the late spring and summer.

The larger woodlot, adjoining the west side of the field, contained about 69 acres, and was of beech-hard maple type. Several areas within it were quite low, and supported heavy growths of *Cephalanthus occidentalis* L. and *Typha latifolia* L., among a variety of plants. Since this woodlot had been ungrazed for a number of years, and since conditions in general were favorable, several species of mammals were abundant. No mammals had been removed by hunting or trapping for a period of years preceding this study. As will be explained further below, the helminths of the mammals resident in this woodlot were rather intensively studied, along with those of the voles from the nearby field.

The voles were trapped from different parts of the area in an effort to distribute the population losses due to trapping evenly over the whole area, thereby minimizing the effort upon vole densities, and, in turn, upon the results obtained. It was the plan to trap 30 voles each month, as well distributed over this period as possible. A total of 345 voles was obtained from the field, over a period of 13 months. Figure 2 shows the age composition of these animals, according to percentage of the total in each weight group.

Observations on the helminths of this area were begun in July, 1945, and were carried on through July, 1946. The voles approached and passed a peak in population density during the time of the study, with the decline occurring

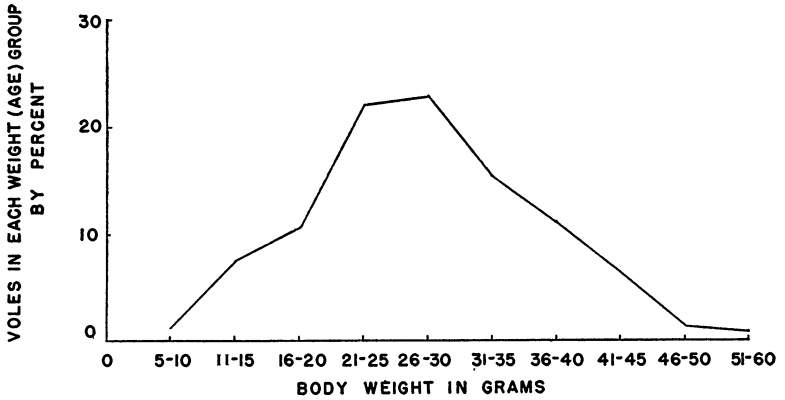

Fig. 2.—Age composition of the 345 voles collected on the southern Michigan study area.

about May, 1946. Observations of others sustained this conclusion. According to Dr. D. W. Hayne (personal communication), this population peak was unusually high — the highest since the year 1937. While no absolute census figure for the area was obtained, it was obvious that the voles were at first very numerous, as attested by well-worn runways, abundant, fresh cuttings, and fecal deposits. Also, the voles could often be seen in places where the vegetation was not too abundant. The high population level persisted through the winter of 1946, but a precipitous decline was noted in the spring, as mentioned above. From the time of the decline on, specimens were obtained only with much difficulty.

The contrast during the late spring of 1946 to conditions of the previous year was indeed great. Runways had become poorly defined from disuse, and cuttings and feces were not to be seen. This population decline took place early, before prolonged dry weather could have reduced breeding activity. No evidence as to the cause of the decline was obtained. In May, 1947, we again trapped in this study area, and it was evident that the vole population was still low. Since no trapping had been done there during the previous year, the population was undisturbed during this period.

The ecology of the helminths of voles, or of any other given host, will never be adequately understood if the particular host in question is the only one examined from areas under investigation. It is probably safe to assume that a mammal resident in a given area must suffer a degree of exposure to helminth species which infect it rarely or not at all. Much can be learned of the interrelationships involved when it is known just which host species and which parasites are present in a given area. We have, therefore, attempted to sample the *total* parasitic helminth fauna of areas studied, whenever it was possible to do so. To date this holds true for areas in Ohio, Michigan, and Wisconsin; there was little opportunity to study other than voles from the areas in Illinois and Indiana. Of the many birds and mammals examined during the course of these studies, most will be considered in future reports. However, additional information is given here for two areas where intensive studies were carried out.

From the Michigan study area (Figure 1, county No. 17), the following resident mammals were examined: opossum, *Didelphis v. virginianus* Kerr; short-tailed shrew, *Blarina brevicauda kirtlandi* Bole and Moulthrop; raccoon, *Procyon l. lotor* Linnaeus; long-tailed weasel, *Mustela frenata noveboracensis* Emmons; skunk, *Mephitis mephitis nigra* Peale and Beauvois; house cat, *Felis domesticus* Linnaeus; woodchuck, *Marmota m. monax* Linnaeus; chipmunk, *Tamias striatus rufescens* Bole and Moulthrop; red squirrel, *Tamiasciurus hudsonicus loquax* Bangs; fox squirrel, *Sciurus niger rufiventer* Geoffroy; eastern flying squirrel, *Glaucomys v. volans* Linnaeus; prairie white-footed mouse, *Peromyscus maniculatus bairdii* Hoy and Kennicott; northern white-footed mouse, *P. leucopus noveboracensis* Fischer; meadow vole, *Microtus p. pennsylvanicus* Ord; pine vole, *Pitymys pinetorum scalopsoides* Audubon and Bachman; house rat, *Rattus norvegicus* Berkenhout; house mouse, *Mus musculus* Linnaeus; jumping mouse, *Zapus hudsonius breviceps* Bole and Moul-

throp; cottontail, *Sylvilagus floridanus mearnsii* Allen. The host names for the Michigan mammals are according to Burt (1946).

Host-parasite relationships as observed on the Michigan study area are shown in Figure 3 (parts A, B, and C). Cestodes, trematodes, and nematodes respectively are tabulated so as to show the host species infected by each parasite, and their relative abundance in these hosts. Only resident mammals trapped in the field or woodlot are considered. It can be expected, in the case of this study area, that the voles were only rarely exposed to helminths infecting some of the mammals living in the woodlot. However, some of the woodlot inhabitants tended to range outward into the surrounding fields. Only two meadow voles were collected well inside the woodlot, and neither was infected with helminths. Only a few mammals were regularly taken in the field, along with the voles; they were jumping mouse, short-tailed shrew, prairie white-footed mouse, and house mouse.

For the intensive study area in Wisconsin, a large marsh of about 350 acres was chosen (Figure 1, county No. 5). This marsh was a rather uniform biotic community, isolated to a considerable degree by the surrounding higher, heavily cultivated agricultural land. A spring-fed creek flowed through the area, and this was further fed by springs arising within the marsh itself. The surface of the smaller creeks bore dense growths of water cress, *Radicula* sp. The marsh vegetation consisted to a large extent of *Phragmites communis* (Reed), *Typha latifolia* L., and *Carex* spp., interspersed with some *Aster* spp., *Solidago* spp., and other plants. The creek banks were grown to willow, *Salix* sp., while other higher areas supported elderberry, *Sambucus canadensis* L., giant ragweed, *Ambrosia trifida* L., and nettle, *Urtica gracilis* Ait.

This area was relatively undisturbed by man, since no hunting or trapping had been done for some years, and it was not used for any agricultural purpose; consequently, mammals were abundant here. This area in some ways was more interesting than the Michigan area, since the voles occurred within the marsh itself, and their contact with the other mammals must have been more immediate.

Although mammals were numerous in the marsh, the number of species here was smaller, limited in this respect by the much more uniform habitat. The following mammals, resident within the marsh, were examined: opossum, *Didelphis v. virginianus* Kerr; short-tailed shrew, *Blarina b. brevicauda* (Say); common shrew, *Sorex c. cinereus* Kerr; raccoon, *Procyon l. lotor* Linnaeus; least weasel, *Mustela rixosa allegheniensis* (Rhoads); mink, *mustela vison letifera* Hollister; skunk, *Mephitis mephitis avia* Bangs; house cat, *Felis domesticus* Linnaeus; woodchuck, *Marmota monax* Linnaeus ssp.; prairie white-footed mouse, *Peromyscus maniculatus bairdii* Hoy and Kennicott; meadow vole, *Microtus p. pennsylvanicus* Ord; muskrat, *Ondatra z. zibethica* Linnaeus; house mouse, *Mus musculus* Linnaeus; cottontail, *Sylvilagus floridanus mearnsii* Allen. In addition to the above, the short-tailed weasel, *Mustela c. cicognanii* Bonaparte, was also resident here, but none of these was collected. The sub-specific status of some of the Wisconsin mammals is not entirely clear at present.

The host-parasite relationships of this marsh were particularly interesting, to a large degree because of the closer contacts of the mammals with one another, as mentioned above. Figure 4 (parts A, B, and C) presents a general picture of these interrelationships. A single house mouse, infected with *Aspiculuris* sp., was collected after Figure 4 was prepared.

Of the mammals present in this area, only the muskrat was rather closely related to the vole (i.e. both of the subfamily Microtinae). If there were any sharing of the helminth parasites by the different host species, one might expect this to occur between the two microtine rodents, while parasite faunas would be shared to a much lesser degree by more distantly related hosts. The results of our examinations indicated that weaknesses in host specificity barriers were not necessarily related to the amount of phylogenetic separation of the hosts.

Thus, we found *Trichuris opaca* Barker and Noyes, 1915, and *Hymenolepis evaginata* Barker and Andrews, 1915, infecting both the muskrat and the vole. The four specimens of the latter cestode taken from voles appeared to be abnormal in development, however, as will be discussed further below. *Entosiphonus thompsoni* Sinitsin, 1931, an abundant parasite of the short-tailed shrew, an insectivore, was encountered in three voles. *Quinqueserialis quinqueserialis* (Barker and Laughlin, 1911) was a common parasite of the muskrat, but did not occur in voles; the latter were commonly infected with a related species, *Q. hassalli* (McIntosh and McIntosh, 1934). *Quinqueserialis hassalli* has been recorded from the woodchuck from the same marsh area (Rausch and Tiner, 1948); however, comparison with specimens collected here from voles indicates that the worms from woodchucks should be considered only as *Quinqueserialis* sp. until additional material is available for study. In general, the findings relative to host specificity appear to parallel those recorded in a previous paper (Rausch and Tiner, 1948). Further data on this are given below, in the discussions of the separate helminth species.

REMARKS ON THE BIOLOGY OF THE HOST

It seems expedient at this point to include some information on the bionomics of voles. This has been obtained mainly from an examination of the literature, although some of our own observations have been included. Most of the observations made by various workers in the United States have been based on the common meadow vole, *Microtus p. pennsylvanicus*. Such information may be of use in better evaluating the results of our investigations.

Voles of the genus *Microtus* are herbivorous mammals, common in both North America and Eurasia. They feed essentially on grasses, and to a lesser degree upon grain, tree bark, tubers, and other vegetable matter. In the North Central States, during the winter months, they are often found in corn shocks. As far as we have been able to learn, voles ingest very little animal matter.

Voles have a characteristic rapid rate of reproduction, and a short life span. According to Hamilton (1937), who studied the common meadow vole, growth is very rapid until about the 12th week, when it is retarded and

the animals are considered mature. Bailey (1924) found that female voles may be sexually mature at 25 days of age, while the males may be fertile at 45 days of age. According to the data presented by Hamilton (1937), age and weight of voles are closely correlated, allowing one to determine rather closely the ages of animals examined. This would be of value if an attempt were made to learn something of the effects of host age on helminth infections in these animals.

The older animals apparently die each year during the late summer or fall, and only the animals born late in the season are able to survive the winter. Baker and Ransom (1938) found, with *Microtus agrestis* L. in Europe, that the older animals die in about October. We have found very few large adults during the winter months over the region where this study was made; the great majority of animals consisted of subadults. We found this to be true even during the times of high population density. We did observe, however, in *Microtus pennsylvanicus drummondii* and *M. ochrogaster,* that large adult animals were present during the winter months of 1947-48, even though the populations were known to be quite low.

Hamilton (1937) listed three factors as contributing to the short life span of the vole: 1) the attainment of sexual maturity at a very early age; 2) extreme prolificacy; 3) little cessation of activity in the search for food. According to the same author (1941), the length of the breeding period of voles in the eastern United States is correlated with population density; breeding may continue on through the winter when the population density is nearing the peak. Hamilton also stated "the number of young in a litter varies with the population level of the mice, large litters predominating when mice are abundant."

Population densities and reproductive activity in voles differ greatly from one area to another at the same time. For example, it was seen, during the winter of 1947-48, that *Microtus p. drummondii,* in Manitoba, and *M. ochrogaster,* in Indiana and Illinois, were breeding at a high rate. This occurred, even though the voles were at a low point in population density. In Wisconsin, on the other hand, where a large number of voles was examined during the same period, not a single large adult was observed. Furthermore, examination of the trapped animals failed to disclose perforate vaginae, placental scars, pregnancy, or evidence of any breeding activity in the males. We are of the opinion, therefore, that nearly all the animals present at this time were nonbreeding adults.

It should not be assumed, however, that these observations on *Microtus p. drummondii* and *M. ochrogaster* are necessarily comparable to those made previously on *M. p. pennsylvanicus.*

RESULTS

The various helminth species obtained are discussed separately below. The numbers in parentheses following the parasite name refer to Figure 1, in which the distribution of the helminths is shown. In showing this distribution, the species of *Microtus* is not considered; however, Table I lists the parasites according to host species in which they occurred, along with certain other data.

CESTODA

In general, cestodes of the family Anoplocephalidae Fuhrmann, 1907, are common parasites of voles, while cestodes belonging to other groups are rare. This appears to be true of the cestodes of Eurasian voles, as well.

ANOPLOCEPHALIDAE

1. *Andrya macrocephala* Douthitt, 1915. (Fig. 1, counties 12, 17, 20, 21).—First described from *Geomys bursarius* (Shaw), this cestode is a common parasite of voles, from which it has been recorded by Rausch (1947). Although *Andrya* spp. have previously been recorded from *Microtus,* specific determinations were not made. Erickson (1938) recorded *Andrya* sp. from *Microtus p. pennsylvanicus* and from *Clethrionomys g. gapperi* Vigors; however, according to his description ("a short broad cestode was removed from the cecum . . ."), he apparently was dealing with a species of *Paranoplocephala* Luehe, 1910.

Another species, *Andrya primordialis* Douthitt, 1915, has also been recorded from voles. Rankin (1945) recorded this cestode from *Microtus longicaudus* (Merriam) and from *M. montanus* (Peale), from the state of Washington. Douthitt (1915) recorded it from *M. p. modestus* (Baird), from Colorado. It seems evident that *A. primordialis* is rare or does not occur in the region where the present study was made.

Although we have not recorded *Andrya macrocephala* from a number of localities from which voles were examined, it is, nevertheless, very common in some areas. Since some of our collections from certain areas were made during the winter months only, when this cestode is rarely found, it is probable that the examination of voles collected during the summer months would show it to be common in other areas also. It might be mentioned here that *Geomys bursarius,* from which it was described, and of which it seems to be a common parasite (Douthitt, 1915) is found only over the western edge of the region considered in this study. Except for a specimen of *Microtus p. drummondii,* which contained 6 worms (5 of which were immature), no more than 4 worms were removed from a single host. The average number per infected animal, based on 345 voles from southern Michigan, was 1.6 worms.

Data obtained from the Michigan study area make apparent certain characteristics of *Andrya macrocephala* infections in the common vole. The peak of infection was observed to occur during the month of August, with very little parasitism by this cestode during the winter months. Figure 5 shows the course of such infections. Immature worms were again found in the spring, suggesting that the infected intermediate hosts are rarely available to the voles during the winter. No differences in age susceptibility were observed.

The life cycle of cestodes of the genus *Andrya* remains unknown, but it would seem likely that mites serve as the intermediate host, in view of our knowledge of the life cycles of other members of the sub-family. The ecology of such mites would be of much importance in the epizootology of the cestodes for which they serve as intermediate hosts. Krull (1939) found that oribatid mites, which serve as the intermediate hosts of *Moniezia, Cittotaenia,* and

others, were most abundant on grass after a heavy rain, and that they retained their greatest constancy where moisture was abundant enough to encourage grass growth. According to the same author, the mites are not reduced greatly by cold, wet weather of a week's duration, or by a dry period of a month's duration, provided these changes occur during the spring or early summer. Krull also found that the mites were more abundant in the spring than in winter, and that they were more abundant on the grass early in the morning than they were during the day. The peak abundance of such mites on grass probably corresponds closely to the period of greatest activity of the voles. It seems probable that mites would often be ingested with the grass upon which voles feed.

It is of interest to note the resemblance of the course of infection of *Andrya caucasica* Kirschenblatt, 1938, in *Microtus socialis,* to that of the present species in *M. p. pennsylvanicus* (Kirschenblatt, 1938; graph 6, page 22). In both cases, infections were low during the winter months. Kirschenblatt also reported a low average number of worms (less than 2) per infected host. One might say that *A. caucasica* in the Transcaucasus region fills an ecological niche very similar to that occupied by *A. macrocephala* in north-central North America.

2. *Andrya microti* Hansen, 1947. (5).—A single cestode referable to this species was collected during February, 1948, at Madison, Wisconsin. Hansen (1947) described *A. microti* from *Microtus ochrogaster* in Nebraska. Recently, through the kindness of Dr. Reinard Harkema, we had the opportunity of examining what appears to be this species from the cotton rat, *Sigmodon h. hispidus* Say and Ord. The infected animals had been collected in Wake County, North Carolina. This species is uncommon in the North Central States region, according to the results of the present study.

There is a striking morphological similarity between *Andrya caucasica* Kirschenblatt and *A. microti;* however, evidence is hardly adequate at present to consider them identical. As far as we have been able to observe so far, cestodes of the genus *Andrya* are not affected morphologically by the host species in which they occur. It seems, however, that the rather closely related species found in North American rodents (*A. macrocephala* Douthitt, 1915); *A. microti* Hansen, 1947; *A. ondatrae* Rausch, 1948) should be carefully studied when a large volume of material becomes available for comparison.

3. *Andrya* sp. (17, 20).—Five specimens of cestodes of the genus *Andrya* were obtained from voles collected in central Ohio and southern Michigan. None of these contained gravid segments, although mature segments were present. The material was not adequate to allow for specific identification, although it is possible that these represented atypical specimens of *A. macrocephala.* Morphologically they did not agree closely with this species, however.

4. *Paranoplocephala troeschi* Rausch, 1946. (1, 4, 5, 6, 8, 16, 17, 18, 21, 22).—Found in or near the cecum of the host, this cestode was the most common found parasitic in voles. Hansen (1947) reported *P. troeschi* from *Microtus ochrogaster* from Nebraska, and it is possible that the previously

mentioned "*Andrya* sp.," recorded by Erickson (1938), was identical with this species.

The maximum number of this species of cestode obtained from a single host was 8, with an average (based on 345 animals from the Michigan study area) of 2.2 per infected animal. As far as could be determined, host age has little or no effect on infections with this cestode. These cestodes appear to be eliminated from the host during the months of early spring (i.e. previous to the first of June).

It was of interest to note that the heaviest infections with this parasite were observed during the winter months, with the highest percentage of animals infected during the months of December and January (see Figure 5).

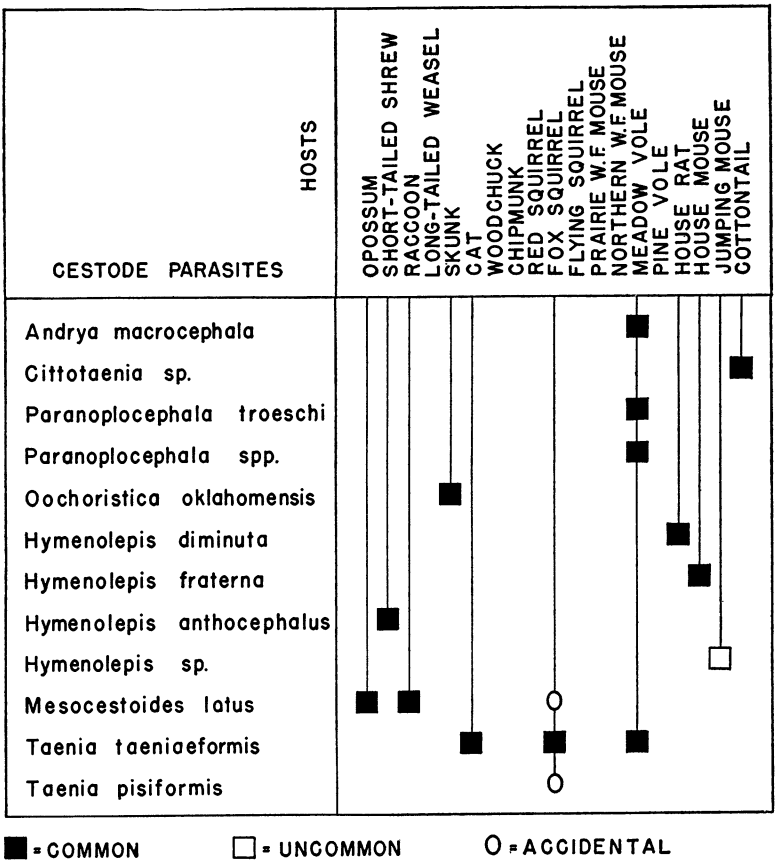

Fig. 3.—Host-parasite relationships on the Michigan study area. Part A. CESTODA.*

* The helminth names used in these charts have been checked, and, as far as could be determined, are valid.

During the course of this study, this cestode was not collected from voles before the month of October, or after the month of May. While occasional infections may occur during the warmer months of the year, they must indeed be rare.

Very small specimens of *Paranoplocephala troeschi,* with only the beginning of strobilae, were found during the earlier part of the winter. It was also noted that immature worms were found in larger numbers in a single host animal than were those with gravid segments. This suggests that only a few worms may be able to survive, even though the initial infection be much heavier. We did not find any immature worms after the month of February. This cestode must mature very rapidly, and must have a very short life span.

It would also seem that mites function as the intermediate host of *Paranoplocephala troeschi,* although there is no definite evidence for such an assumption. It appears that the intermediate host of this cestode is not available to

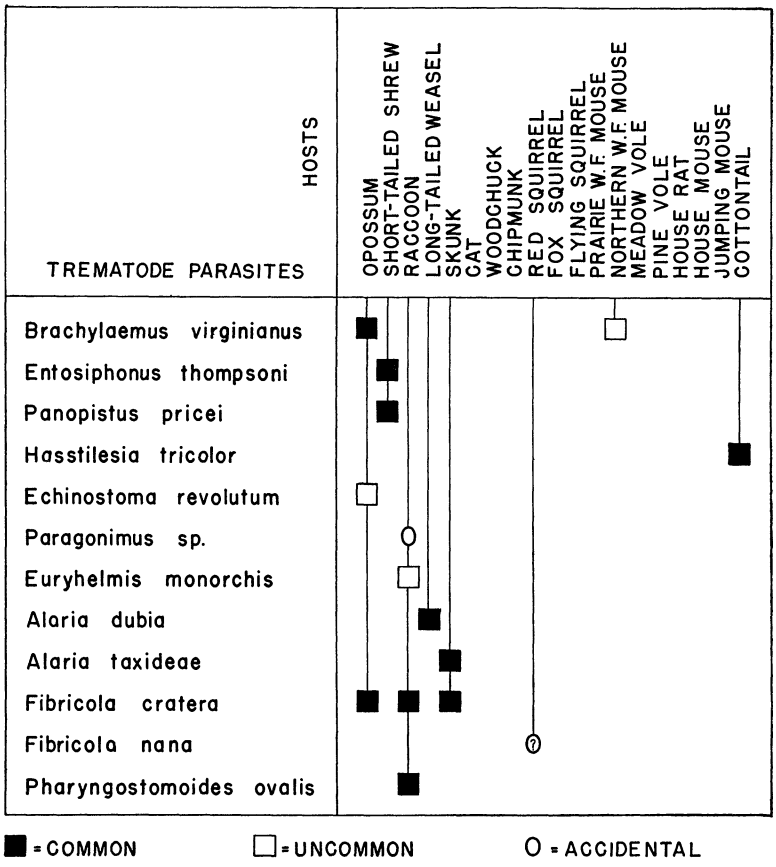

Fig. 3.—Host-parasite relationships on the Michigan study area. Part B. TREMATODA.

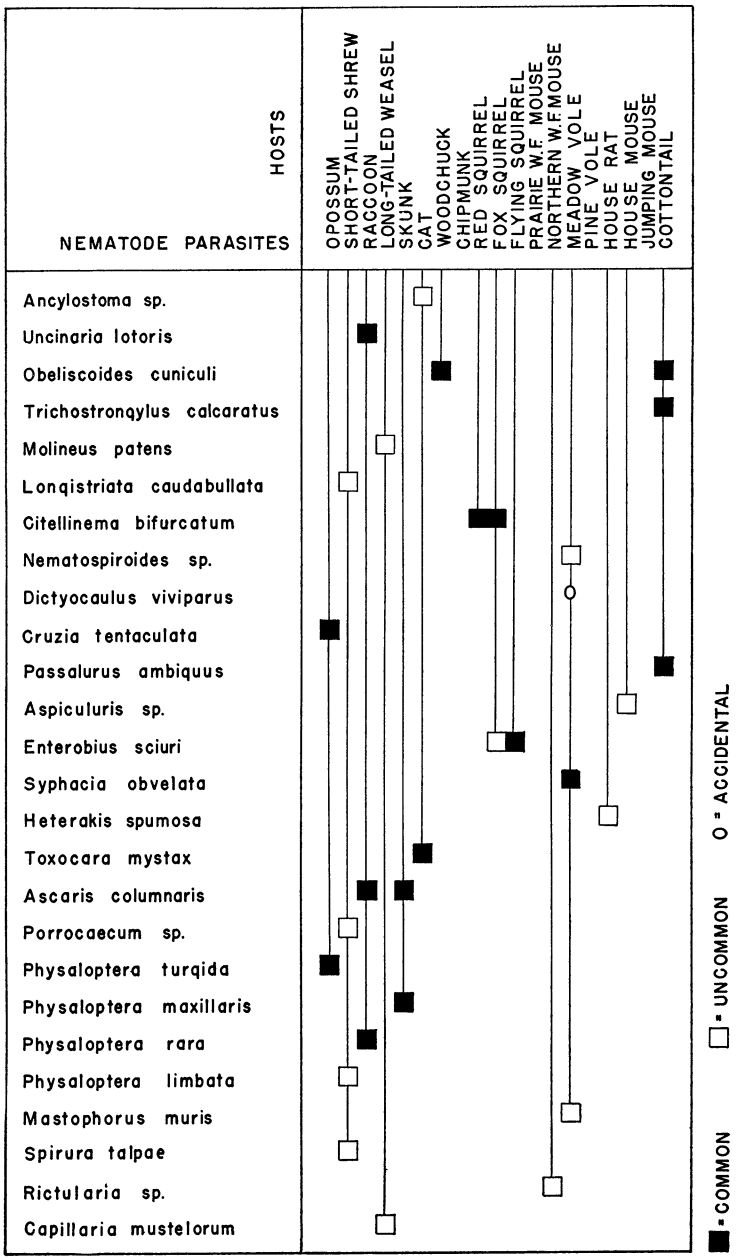

Fig. 3.—Host-parasite relationships on the Michigan study area. Part C. NEMATODA.

the voles during the warmer months of the year, and this is suggestive of some very interesting ecological factors upon which this must be dependent. Whether these factors are connected with seasonal variation in host behavior, or with physiological or immunological peculiarities of the definitive host, is unknown.

Paranoplocephala troeschi is morphologically very close to *P. brevis* Kirschenblatt, 1938. Although Kirschenblatt's paper was cited at the time *P. troeschi* was described (Rausch, 1946), it was not yet avalaible. It can be seen that these worms appear to fill similar ecological niches in their respective regions of distribution, and this may be very important in establishing relationships. Kirschenblatt's graph 3 (page 18) gives some information on the behavior of *P. brevis* in the host (*Microtus*). It is probable that further study will show that *P. troeschi* should be considered a synonym of *P. brevis*; however, additional material for comparison is needed to establish this.

5. *Paranoplocephala* spp. (1, 2, 3, 4, 5, 10, 12, 14, 16, 17, 18, 21, 22).—When *P. troeschi* was described the attendant examination of a fairly large series of cestodes from voles revealed that specific differences often were most difficult to delineate in the genus *Paranoplocephala*. This, with the present confusion of names, would indicate that further work on this group is badly needed. We expect to present further data on this problem in the future. Because of the present status of these cestodes, specific determinations are not indicated here.

A large species of *Paranoplocephala* was occasionally found in the duodenum of the host, just below the stomach. In no case was more than a single worm found per host animal. What appears to be another species was found lower in the small intestine. In general, these cestodes were uncommon in voles, and nothing was observed concerning their epizootology.

DILEPIDIDAE

6. *Choanotaenia* sp. (12).—A single worm belonging to the genus *Choanotaenia* Railliet, 1896, was removed from the intestine of a specimen of *Microtus ochrogaster,* collected at Champaign, Illinois. The hooks appeared to be 26 in number, and were arranged in a double row; they averaged 30 μ in length. The testes averaged 31 in number, and the cirrus sac measured from 80 to 115 μ in length. No gravid segments were present. This may represent an accidental infection.

HYMENOLEPIDIDAE

7. *Hymenolepis fraterna* Stiles, 1906. (21).—A single cestode, without a scolex, was obtained from a vole collected near Marysville, Ohio. It seemed to agree in all respects to *H. fraterna. Hymenolepis fraterna* was commonly seen as a parasite of the house mouse, but it cannot be considered a common parasite of the voles of this region. Hughes (1940) recorded this cestode as occurring in a European vole, *Microtus agrestis* L., however.

8. *Hymenolepis evaginata* Barker and Andrews, 1915. (5).—Two voles,

each containing two cestodes of this species, were collected on the southern Wisconsin study area. Although a common parasite of muskrats over the North Central States region, it must be considered accidental in voles.

The cestodes from the voles were rather small for this species (80 to 130 mm), but in general were typical in their morphology. However, it was noted that in no case had any eggs developed, although proglottids had been shed from all four strobilae. This is perhaps further evidence that the vole is an abnormal host for this parasite.

9. *Hymenolepis* sp. (13).—Five specimens of a cestode belonging to this genus were obtained from a vole collected in eastern Illinois. Unfortunately, the hooks had been lost from the scolices, and the material is not considered adequate for specific identification.

TAENIIDAE

10. *Taenia taeniaeformis* (Batsch, 1786). (1, 8, 12, 17, 22).—Strobilocerci of this cestode were rather common in the liver of voles from some areas. The distribution was, however, quite local. This is not readily understood, since there must be little difference in the house cat population over the region under consideration. Feral cats were present over most of the areas considered, and, in most cases, vole habitat areas were readily accessible to cats from nearby farms. In northern Wisconsin (Figure 1, number 1) where rather a high incidence of infection was observed, it is possible that the bobcat, *Lynx rufus* Schreber, might also have acted as the definitive host for this cestode. Rollings (1945) reported *Taenia taeniaeformis* to be a fairly common parasite of the bobcat in Minnesota. No information is yet available on Wisconsin bobcats.

On the Michigan study area these larval cestodes were first seen in voles in November, and during each month thereafter until the last of May. The largest percentage of infected animals was seen during the month of January. A somewhat parallel situation was observed in the fox squirrel, concurrently trapped in the adjacent woodlot, although a smaller number of animals was infected (Rausch and Tiner, 1948). In the voles from this area the maximum average number of cysts per animal per month coincided with the peak in incidence of infection. Although this parasite was found in the liver of a muskrat from the southern Wisconsin study area, it was not observed there in voles. Feral house cats, collected on the immediate study area, were found to be infected with cestodes of this species, and other cats, not captured, were from time to time seen on the area.

A total of 26 house rats was examined from a farm in central Ohio, and it was found that 21 of these were infected with larval cestodes of the present species. A total of 35 voles examined from the same farm area failed to disclose any infections by this parasite. Egg density per given unit area probably decreased very rapidly as distance from the farm buildings increased. Unfortunately, enough rats living in the fields away from the buildings could not be obtained to allow for a comparison under these conditions.

A cysticercus belonging to the genus *Taenia* was taken from the liver of a specimen of *Microtus p. drummondii,* collected near Winnipeg, Manitoba.

This cysticercus was not identified to species. Two rows of hooks were present, with 12 in each row. The larger hooks averaged 72 μ in length, while the smaller ones averaged 49 μ.

11. *?Cladotaenia* sp. (5, 13, 17, 21).—A few voles were found to be infected with very small cysticerci, which occurred in the liver. Two specimens from voles collected in southern Michigan had hooks about 16 μ in length, arranged in a double row.

On the southern Wisconsin area, a relatively heavy infection was noted. Of the 43 voles taken on the marsh, 12 were infected, with an average of 3 cysts per infected animal. The hooks of these, also arranged in a double row, measured about 23 μ in length. The liver cysts were quite small, and commonly measured about 2 mm. in diameter. With the possible exception of one muskrat, no other host animal from this area was found infected by these cysticerci.

It is possible that these cysticerci were larval cestodes of the genus *Cladotaenia*; it is hoped that this can be determined by feeding experiments with hawks. In the Wisconsin marsh, hawks (*Circus, Buteo, Accipiter*) were usually abundant, and perhaps conditions in this area allowed a better opportunity for vole infections with this parasite. Experimental work by one of us (R. R.) has shown that these cysts are not larvae of owl cestodes (*Paruterina*); this work will be reported separately.

TREMATODA

During the course of the present study, only two species of trematodes were found which could be considered natural parasites of voles. One of these, *Quinqueserialis hassalli* (McIntosh and McIntosh, 1934), was widely distributed, and occurred in a number of localities where habitat seemingly was favorable to the intermediate host. A second, *Mediogonimus ovilacus* Woodhead and Malewitz, 1936, was recorded only from Washtenaw County, Michigan, from which locality it was first described. Three infections by a third species, *Entosiphonus thompsoni* Sinitsin, 1931, could only be regarded as accidental. Price (1931) reported *Microtus pennsylvanicus* to be the natural host for *Schistosomatium douthitti* (Cort, 1915); it is possible that we have overlooked infections of this parasite.

That voles have few trematode parasites is not surprisinig, considering their diet, and the fact that in general they inhabit areas which are not favorable habits for snails.

NOTOCOTYLIDAE

12. *Quinqueserialis hassalli* (McIntosh and McIntosh, 1934) (4, 5, 15, 18, 21).—The only common trematode found in voles, this species appeared to be abundant only locally, although it has been recorded from voles over a wide geographical area (Harwood, 1939). The distribution of this parasite seems to be limited to areas with aquatic habitat suitable for a snail intermediate host.

On the southern Wisconsin marsh, a high percentage of voles (46 per cent) was infected. The trematodes averaged 8 per infected host, with a maximum number of 37 in a single host. Muskrats were not found to be infected with

this parasite; they were, however, heavily infected with a member of the same genus, *Quinqueserialis quinqueserialis* (Barker and Laughlin, 1911). The latter occurred in very large numbers (average for 6 infected muskrats: 406 worms). More than a thousand of these trematodes were removed from the cecum of a single muskrat.

Voles trapped on the Wisconsin marsh during the winter months were found to be heavily infected by *Quinqueserialis hassalli*. Whether these infections had carried over from the previous fall, or whether they obtained during the winter months, is not known. A few immature trematodes found during January and February indicated that infective stages were available to the voles to at least some degree during the winter. It might be mentioned here that open water was always present in this marsh, because of the continual flow from the springs. Although the investigation here has so far been carried through only one spring season, evidence so far would indicate that there is a decrease in infection by this parasite during this time.

PLAGIORCHIIDAE

13. *Mediogonimus ovilacus* Woodhead and Malewitz, 1936. (18).—Two of four voles secured from Washtenaw County, Michigan, were infected by this helminth. This species appears to be very restricted in its distribution, since we did not encounter it elsewhere in the region considered. In one case, more than 50 worms were taken from cysts in the liver of a young vole (28 grams), while 3 specimens were taken from the bile duct of a second animal. In the first case, a few of the trematodes had migrated through the bile duct into the small intestine, probably after the death of the host. Our observations on this species agree with those made by Woodhead and Malewitz (1936). We observed also that the mature worms in the case of the heavier infection were much smaller than were those from the bile duct of the second animal. The infected animals were captured along a river.

Part of the liver of the animal showing the heavier infection was sectioned, and a few observations were made on the reaction of the host tissue to this parasite. The worms had been well walled off, and were surrounded by a capsule of connective tissue. Many eggs, found outside the capsule, were also being walled off, and a heavy deposition of a black pigment was seen in the area with the eggs. There was a metaplasia of the biliary epithelium, and some pressure necrosis of the liver cells. The cellular reaction was moderate, consisting mainly of macrophages. Eosinophiles were not observed. This appeared to be the most pathogenic parasite encountered by us during the course of the present study, although it does not seem probable that there would be any serious result to the host, unless infections were extremely heavy. A photomicrograph of a typical liver section is given in Figure 6.

BRACHYLAEMIDAE

14. *Entosiphonus thompsoni* Sinitsin, 1931. (5).—This trematode was taken only from the voles of a single locality, and must be considered purely accidental in the vole. Two of the infected voles contained a single worm each,

while a third harbored two worms. The worms appeared to be normal in development; all were mature, with numerous eggs in the uteri.

Entosiphonus thompsoni was a very common parasite of the short-tailed shrew over the entire region considered in this study. However, the short-tailed shrew was not abundant in the marsh from which the infected voles were taken. Another shrew, *Sorex c. cinereus,* was quite abundant in the area, but only on one occasion was this species found to be infected with *E. thompsoni*; in this case, a few small, immature worms were collected. Krull (1933) has recorded this trematode from the white-footed mouse, *Peromyscus leucopus noveboracensis.*

NEMATODA

Nematodes were found to be very common parasites of voles, although they differed considerably in variety and number from one area to another.

TRICHOSTRONGYLIDAE

15. *Nematospiroides* sp. (5, 17, 18).—This nematode was taken from 9 animals of the 345 examined from the southern Michigan study area, and from 27 of the 43 voles from the Wisconsin study area. In general, it was an uncommon parasite. The number of worms per infected host was much higher in the Wisconsin area, ranging from 1 to 178 (average: 13), while in the Michigan area it ranged from 3 to 31 (average: 6) per infected host.

Dikmans (1940) described two North American species of *Nematospiroides,* bringing the number in the genus to 3. Unfortunately, our specimens do not agree with any of the described species. They appear to be nearest to *N. carolinensis* Dikmans, 1940, in that they possess a separate dorsal ray in the bursa, and have spicule lengths ranging from 1.9 to 2.4 mm. long in males which were 5.1 to 7.4 mm. in length. *Nematospiroides carolinensis* was described from *Clethrionomys* from North Carolina. No nematodes of this genus were found in any other hosts collected from the marsh where the heavy infections occurred in *Microtus,* although *N. longispiculatus* Dikmans, 1940, was found in both muskrats and voles collected in Washington, D. C., and in New Jersey (Dikmans, 1940).

Spurlock (1943) did some experimental work with the related species *Nematospiroides dubius* Baylis, which occurs as a parasite of house mice and other rodents. He found that some strains of laboratory mice were more susceptible than others, but was unable to draw any conclusions concerning acquired resistance. When large numbers of larvae were given, the mortality was high. The infection with this species of helminth apparently lasts for at least 8 months.

Spurlock also found that after the eggs of *Nematospiroides dubius* hatch, the free-living stage is passed in moist fecal material. The larvae are infective about 6 days after the deposition of the feces, and are found at that time on the surface of the fecal mass. Kirschenblatt (1938) has given further observations on the development of *Nematospiroides* larvae in *Microtus.*

Elton, Ford, and Baker (1931) studied the parasites of some European rodents, and found *Nematospiroides dubius* to be a common parasite of the

woodmouse, *Apodemus sylvaticus,* but did not find it in either *Clethrionomys* or *Microtus.* In 692 specimens of woodmouse, they found an incidence of infection of 85 per cent in adult animals. They also reported a high incidence during the summer and early autumn. The seasonal variation in incidence of infection with *N. dubius* was directly dependent upon age distribution of the animals, and, therefore, directly correlated with the breeding cycle. The question arises whether this is also true of the course of infection in *Microtus.*

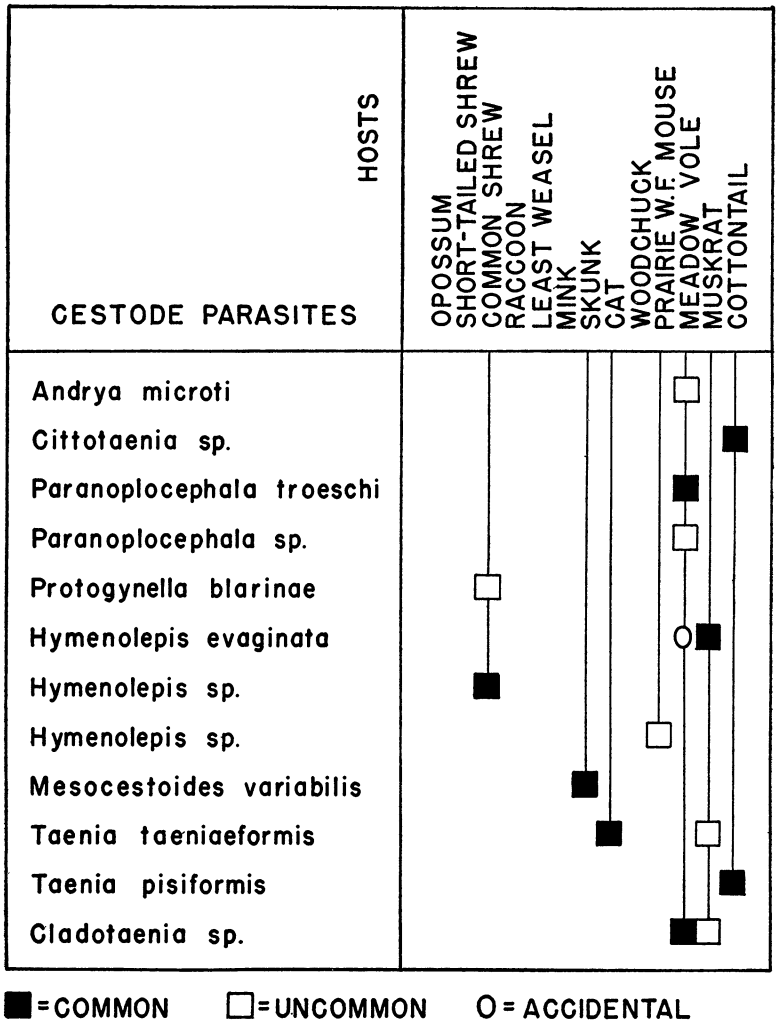

Fig. 4.—Host-parasite relationships on the Wisconsin study area. Part A. CESTODA.

Erickson (1944) reported that, in the snowshoe hare, *Lepus americanus* Erxleben, the helminth parasites are most abundant during the peak of the population cycle of the host. Elton, Ford, and Baker (1931) found that there was a higher percentage of woodmice infected by *Nematospiroides dubius* at the time of high density just before the mortality occurred, but no unusual increase in number of worms per infected animal.

Kirschenblatt (1938) found, with the same parasite, also in the woodmouse, that the number of worms ranged from 11 to 86, with an average of 34 per infected animal. He found larger infections in mountain forest areas than in open country, and considered the moist woods to be more suitable

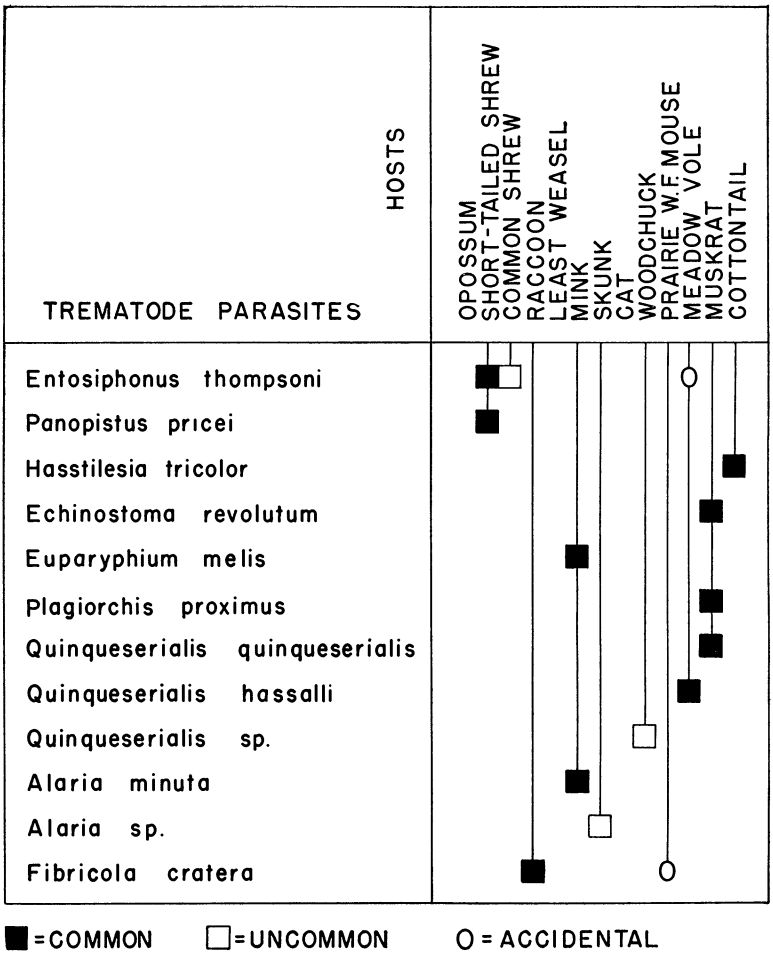

Fig. 4.—Host-parasite relationships on the Wisconsin study area. Part B. TREMATODA.

habitat for larval development. We observed heavier infections and a higher incidence of infection in the southern Wisconsin area, where the habitat was much wetter than in the Michigan area. Our observations seem to agree with those of Pearse (1930) in respect to the general relation of the helminths to the habitat of the host. It is of interest that we have never taken this nematode from animals of any species which were trapped within forest areas.

We have not yet examined enough infected voles to allow any observations on age susceptibility. Elton, Ford, and Baker (1931) showed, in the woodmouse, that the infection with this nematode increases with the age of the host.

16. *Longistriata dalrymplei* Dikmans, 1935. (4).—Although it has been reported from several localities (Dikmans, 1935), this nematode was found to be uncommon in the voles of the region considered here. Infected animals were taken only at Horicon Marsh, Wisconsin, from *Microtus p. pennsylvanicus*. Other foci of infection may occur in the region studied, but, if so, they were overlooked because of the relatively small number of animals examined.

The life cycle of a related species, *Longistriata musculi* Dikmans, 1935, has been studied by Schwartz and Alicata (1935), and it was found that larvae may gain entrance to the host either by way of ingestion or through the skin.

It seems probable that voles can withstand fairly heavy infections with this parasite, without serious result. The infections we observed were medium; the maximum number of worms seen in a single host was 48.

17. *Dictyocaulus viviparus* (Bloch, 1782). (17).—Two males and a single female, the latter containing many embryonated eggs, were recovered by one of us (R. R.), apparently from the cecum of a vole from southern Michigan. Before the worms were fixed, the absence of a separate dorsal lobe in the bursa and the heavy spicules of the males were noted. The problem of identification was transmitted to the junior author. The finding of bursate strongyloid worms in the intestinal tract suggested that they belonged to the family Trichostrongylidae Leiper, 1912. Detailed drawings were made, and a search through the literature was undertaken in an effort to determine their systematic position. This proved to be quite without result until similarity was noticed between the dorsal rays of the bursa in our drawings and those of Dikmans (1936; Fig. 1, No. 11). A subsequent comparison of our specimens with *D. viviparus* from domestic cattle indicated that they belonged to this species. Our material was then sent to Dr. Dikmans, who replied that he could only confirm the identification.

Both Dr. Dikmans and Dr. G. R. LaRue cautioned the authors that contaminated equipment or faulty labeling might have been a source of error. However, cattle were not autopsied in the same building where the voles were examined, and petri dishes used by us were used in addition only for bacteriological purposes. The fact that the worms were studied while still alive seems to preclude any possibility of faulty labeling. We had no doubts as to their source while in the process of identifying them. We feel obliged to as-

sume, therefore, that the worms actually were present in the intestinal tract of the vole.

It would seem that the vole had ingested the worms as larvae, and that

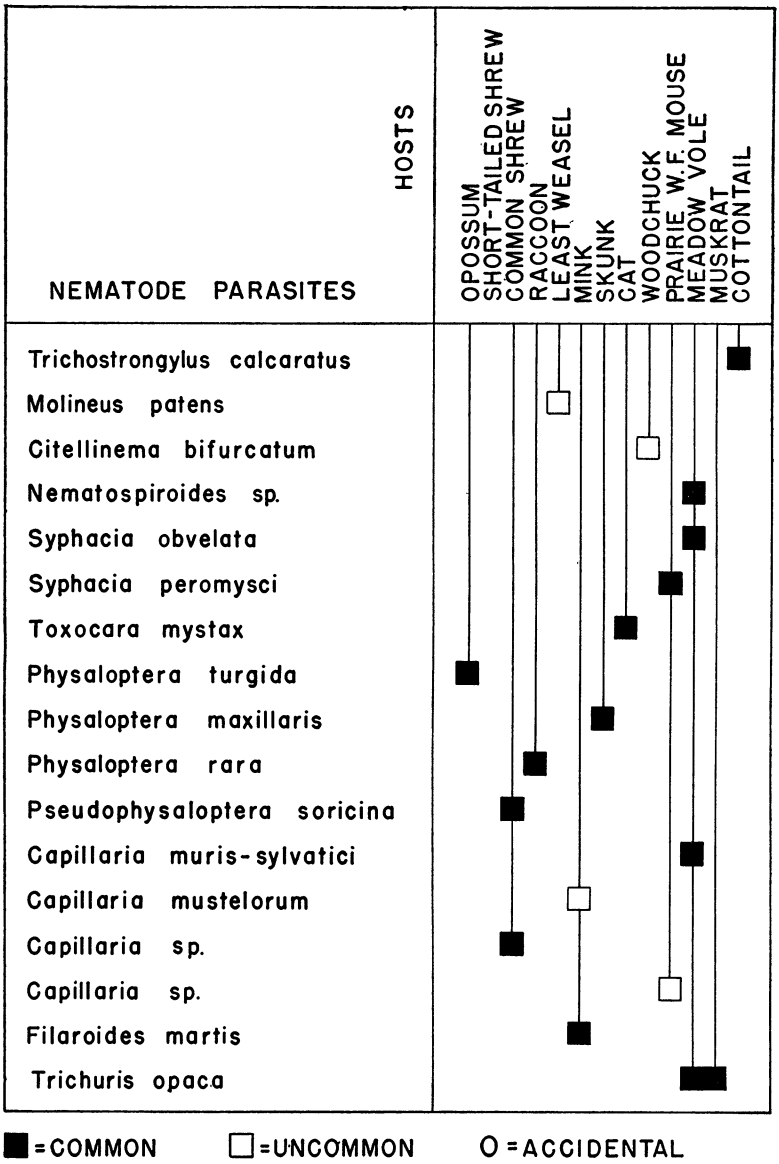

Fig. 4.—Host-parasite relationships on the Wisconsin study area. Part C. NEMATODA.

they had grown to maturity in its cecum. Since voles reduce their food to rather small size before it reaches the stomach, it does not seem likely that such large worms could have been ingested intact. Beef cattle were pastured in the same field where the vole was collected. We do not know if these animals were infected with *Dictyocaulus viviparus*.

It is of interest that Dougherty (1946) has decided that there is morphological evidence for classifying the genus *Dictyocaulus* in the Trichostrongylidae.

OXYURIDAE

18. *Syphacia obvelata* (Rudolphi, 1802). (1, 2, 3, 4, 5, 7, 8, 12, 13, 15, 16, 17, 18, 20, 21, 22).—The most common helminth encountered in the voles of this region, *S. obvelata* was widely distributed. It was also recorded from *Microtus pennsylvanicus drummondii*, from near Winnipeg, Manitoba, and was observed in the house rat in Michigan, Ohio, and Wisconsin, and in the house mouse in Illinois.

The life cycle of this nematode is direct (Lawler, 1939), and there does not appear to be any immunity developed, age or otherwise, according to what has been learned from work with other rodents (Culbertson, 1941; Taliaferro, 1929).

Syphacia obvelata was found throughout the year. On the southern Michigan study area, it was found, during the first summer, that relatively few animals were infected, but the average number of worms was high. Later, during the winter, a large proportion of the population was infected, but with a lower average number of worms per infected animal. Of the 345 voles collected from this area, 30 per cent were infected with this parasite. The average number of worms per infected animal was 15.5, with a maximum number of 242 worms occurring in a single host. On the Wisconsin area, where the habitat was much wetter, 30 per cent of the animals also were infected. In this latter area, *Syphacia peromysci* Harkema, 1936, occurred commonly, and apparently was parasitic only in *Peromyscus* spp.

Kirschenblatt (1938; graph 12, page 36) found the peak of infection during the spring, in *Microtus*, with the maximum average number of worms per animal at this time, also. He observed two peaks of infection, one in the spring and one in the fall, in *Mus musculus* subsp. *Syphacia stroma* (von Linstow, 1884) showed, in the woodmouse, a behavior similar to that of *S. obvelata* in *M. musculus* subsp.

Male worms were rare, a condition previously noted by other workers (Hall, 1916), but in a few cases a majority of worms was males. Kirschenblatt (1938; page 36) stated "I found males more than once, and furthermore in some cases the number of males exceeded the number of females. Frequently it happened that the males were not found in the presence of females. The males of *S. obvelata* do not appear to be a rarity, as it seems that one would judge from the data of Linstow, Hall, and Schultz. But evidently they live a considerably shorter period than the females. It was impossible to establish any rule as to the relationship of the number of males to the females in the various seasons of the year. The absence of males seems especially strange in the comparatively large material that Schulz had. One

cannot escape the thought that the males as a result of their small size were lost in the washing of the gut with water, according to the method of helminthological investigation of Skrjabin, or they burst in the water and were useless for further systematic study."

SPIRURIDAE

19. *Mastophorus muris* (Gmelin, 1790). (17).—An uncommon parasite of voles of this region, *Mastophorus muris* (=*Protospirura muris*; see Chitwood, 1938) was found only in southern Michigan, and occurred in only 2 per cent of the 345 animals examined from this study area. This helminth was collected during the winter, spring, and summer of 1946. According to Hall (1916) after Leuckart (1867) and Marchi (1871), the eggs of *M. muris* are ingested by beetles of the genus *Tenebrio,* and in five weeks encapsulated larvae are found in the body cavity. Baylis (1931) stated that meal beetles and a cockroach, *Blatella germanica* (L.), probably act as the intermediate hosts for *M. muris* near human habitations, but that other insects probably replace them in more remote areas. Whether or not voles purposely ingest such insects is not definitely known.

Kirschenblatt (1938) stated the length of life of these worms is comparatively long, apparently not less than a year, and that the number of worms does not depend upon definite seasons.

In the few voles infected with this parasite, no evidence of any pathogenicity was observed, since neither local lesions nor deteriorated physical condition of the host were evident. Lesions such as those caused by *Physaloptera* spp. in some of their respective hosts were in no case evident in the stomachs of the infected animals. The heaviest infection, with 17 large female and 3 male worms, was observed in a female vole. This animal, collected on July 21, 1946, weighed 63 grams, and contained 9 nearly full-term fetuses. The average number of worms, for the five infected animals, was 7.

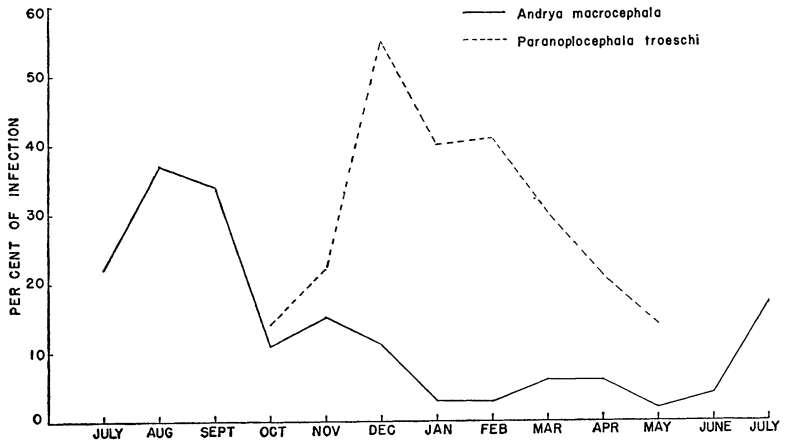

Fig. 5.—Seasonal variation in *Andrya macrocephala* and *Paranoplocephala troeschi* infections in voles. Based on 345 voles examined from the Michigan study area.

TRICHURIDAE

20. *Capillaria muris-sylvatici* (Diesing, 1851). (5).—We know little so far about this nematode, which was recorded from a single area in Wisconsin. We are indebted to Mr. Clark P. Reed, Rice Institute, for the identification of nematodes of the genus *Capillaria*. This species was not recorded from hosts other than voles.

Although accurate counts were difficult, infections with *Capillaria muris-sylvatici* apparently consisted of up to about 40 worms. The data given by Kirschenblatt (1938) on members of the genus *Capillaria* from Russian rodents might be mentioned here. He gave information on *C. hepatica* Bancroft, 1893, in the snow-mouse, *Chionomys nivalis* Mart., and on *C. gastrica* Baylis, 1926, in *Microtus socialis*. He stated (page 30) that "young infected specimens (of *Microtus*) weighing from 21 to 27 grams were found only in February; in the rest of the year only old infected animals were encountered. Evidently the duration of the life of the worm is great, therefore the extensiveness of the infection increases with age." The same author observed a similar behavior of *C. hepatica* in *Chionomys* (graph 8, page 28).

21. *Trichuris opaca* Barker and Noyes, 1915. (5, 18).—Whipworms which belonged to this species were collected from both the vole and the

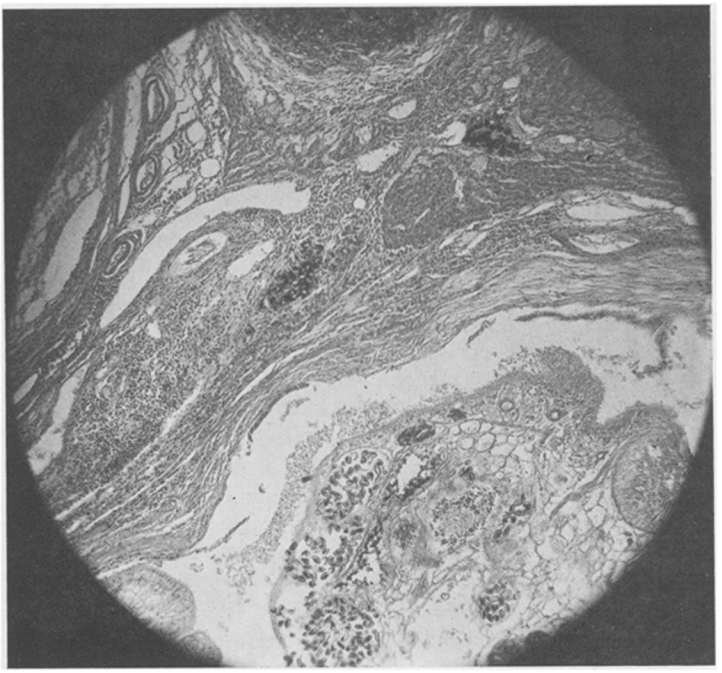

Fig. 6.—Photomicrograph of a liver section from a vole infected with *Mediogonimus ovilacus*. ×70.

muskrat from the southern Wisconsin marsh area, and from a vole from southern Michigan. Of the animals examined, the voles harbored a larger number of worms per infected animal than did the muskrats; however, a much larger number of voles was examined. Of the 43 voles from the marsh area, 11 were infected, while 4 of the 6 muskrats examined were infected. Infections in the former host ranged from 1 to 26 (average: 9.6) per infected animal, while in the muskrat infections ranged from 2 to 12 (average: 4.6) per infected animal.

Records of *Trichuris* from the muskrat do not appear to be numerous. Dr. E. W. Price informed us that the U. S. National Museum Helminthological Collection has only a single vial of whipworms from the muskrat, collected in Maryland. It appears to us that the vole may be a more important host for *T. opaca* than is the muskrat.

Hall (1916) has pointed out that there is a discrepancy between the measurements in Barker's drawings and text. Through the courtesy of Dr. H. W. Manter, University of Nebraska, type specimens of *Trichuris opaca* were made available to the writers. Figures 1 and 3 are essentially correct, and are drawn to the same scale, although the cloacal tube of the male in Figure 1 was confused with the spicule. No specimens could be found which corresponded to Figure 2, but it shows more accurately than Figure 1 the details of the posterior end of the male, provided that the scale (Figure 2) is changed to read approximately ".37 mm." The spicule length given in the text should be corrected to read "1.35 mm." Additional work will be necessary to adequately redescribe *T. opaca,* and to determine its affinities with other species of *Trichuris* from rodents.

22. *Trichuris* sp. (9, 11).—In addition to the aforementioned *T. opaca,* females of a *Trichuris* sp. were collected from *Microtus ochrogaster* in Illinois. The absence of male specimens prevented our determining their specific identity.

DISCUSSION AND CONCLUSIONS

From the foregoing material, it is evident that much is yet to be learned concerning the helminths parasitic in voles, to say nothing of the parasites of wildlife in general. However, only long-term studies can make substantial contributions toward solutions of the basic problems involved. At present, nothing definite can be said concerning the effect of helminth parasites on population fluctuations of rodents.

During the course of our work we have not been able to observe any definite connection between population density of voles and parasite density. Both quantitative and qualitative differences in helminth infections appear to be seasonal or geographical in nature. This opinion is sustained by the previous work on the helminths of sciurids (Rausch and Tiner, 1948).

One is much impressed by the localized nature of infections with certain helminths over the North Central States region. This is especially marked in the case of certain vole parasites, such as *Trichuris opaca, Mastophorus muris, Capillaria-muris sylvatici, Longistriata dalrymplei,* and *Mediogonimus*

ovilacus. This phenomenon was pointed out by Kirschenblatt (1938), and was stated as follows in his summary: "Dabei hatte es sich erwiesen, dass die Invasion der mäuseähnlichen Nagetiere mit Parasiten nicht nur in verschiedenen Ortschaften eine verschiedene ist, sondern sich auch in verschiedenen Kolonien in ein und derselben Ortschaft unterscheidet. Die Unterschiede in der Invasion der Nagetiere aus einer Kolonie werden im Allgemeinen durch die Altersunterschiede verursacht und hängen von der Jahreszeit ab." He stated further that: "Die Helminthen-fauna der mäuseähnlichen Nagetiere in der Umgebung von Tbilisi ist im Frühling (Mai) am reichsten und am verschiedenartigsten, im Sommer (Juli) dagegen am ärmsten und am wenigsten verschiedenartig. Sommerhitze und Trockenheit hemmen die Invasion der Nagetiere mit den meisten Helminthen-Arten. Deshalb stellt der Sommer in den Steppen Transkaukasiens eine solche Jahreszeit dar, während welcher die Nagetiere sich spontan von den meisten Helminthen befreien."

The occurrence of *Nematospiroides* sp., *Trichuris opaca,* and *Capillaria muris-sylvatici* in the isolated marsh in southern Wisconsin, and their apparent rarity in the surrounding areas, may be evidence of environmental influence. The importance of habitat in the case of certain other helminths is self-evident. As has been noted by other writers, anoplocephaline cestodes occur most abundantly in animals from areas suitable to free-living mites; the heaviest infections being observed in animals from areas with heavy stands of grass.

With the exception of *Mediogonimus ovilacus,* we were unable to determine that the helminths parasitic in voles had any deleterious effect upon the host. Evidence seems to substantiate results obtained from the study of sciurid helminths (Rausch and Tiner, 1948)—i.e. many helminths probably can be considered innocuous when the host is living in its natural state; many of these should possibly be considered more nearly commensals than parasites.

It was noted that there was a greater number and variety of helminths present in the northwestern part of the region considered, with fewer in the eastern and southern parts. This was also observed in the case of the sciurid parasites. It may be that drainage and heavy cultivation of the southeastern part of the region has exerted considerable influence on some of the vole parasites, which appear to require a fairly wet habitat. However, the number of hosts so far examined is hardly large enough to allow any conclusions concerning helminth distribution.

Not only can new host- and new distribution records be obtained from nearly every area where intensive studies are made, but new species are also often found, indicating that our knowledge of the North American helminth fauna is still quite incomplete. Especially is little known of the epizootology of helminths parasitic in wild birds and mammals, and in connection with this, there is much opportunity to make valuable observations on the basis of season-to-season studies.

SUMMARY

A total of 648 voles of three species, collected since 1942 from the states of Ohio, Indiana, Illinois, Michigan, Wisconsin, and from Manitoba, has been examined for helminth parasites. Special reference has been made to host-

parasite relationships, and detailed information has been given for two areas where intensive studies were made.

A total of 21 species of helminths was collected, some of which are recorded from voles for the first time. The helminth species encountered have been discussed separately in the text.

Information has been given on seasonal variation in infections with certain helmiths. There is evidence that season of the year and geographical location have much influence on kind and number of helminths parasitic in voles. As far as we have been able to determine, most of these vole parasites have little or no harmful effect upon the host.

TABLE I.—Summary of Results.

Host	No. examined	Parasite	No. infected
Microtus p. pennsylvanicus	570	*Andrya macrocephala*	59
		Andrya microti	1
		Andrya sp.	4
		Paranoplocephala troeschi	90
		Paranoplocephala spp.	32
		Hymenolepis fraterna	1
		Hymenolepis evaginata	2
		Taenia taeniaeformis	43
		Cladotaenia spp.	13
		Quinqueserialis hassalli	21
		Mediogonimus ovilacus	2
		Entosiphonus thompsoni	3
		Nematospiroides sp.	32
		Longistriata dalrymplei	3
		Dictyocaulus viviparus	1
		Syphacia obvelata	145
		Mastophorus muris	6
		Capillaria muris-sylvatici	18
		Trichuris opaca	11
Microtus p. drummondii	32	*Andrya macrocephala*	1
		Taenia sp.	1
		Syphacia obvelata	3
Microtus ochrogaster	46	*Andrya macrocephala*	5
		Paranoplocephala sp.	9
		Choanotaenia sp.	1
		Hymenolepis sp.	1
		Taenia taeniaeformis	1
		Cladotaenia sp.	1
		Quinqueserialis hassalli	1
		Syphacia obvelata	13
		Trichuris sp.	2

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